Rigid patterns of synchrony for equilibria and periodic cycles in network dynamics

Martin Golubitsky[1] and Ian Stewart[2]
[1]Mathematical Biosciences Institute, Ohio State University, Columbus, Ohio 43210, USA
[2]Mathematics Institute, University of Warwick, Coventry CV4 7AL, United Kingdom

(Received 3 February 2016; accepted 18 April 2016; published online 23 June 2016)

We survey general results relating patterns of synchrony to network topology, applying the formalism of coupled cell systems. We also discuss patterns of phase-locking for periodic states, where cells have identical waveforms but regularly spaced phases. We focus on rigid patterns, which are not changed by small perturbations of the differential equation. Symmetry is one mechanism that creates patterns of synchrony and phase-locking. In general networks, there is another: balanced colorings of the cells. A symmetric network may have anomalous patterns of synchrony and phase-locking that are not consequences of symmetry. We introduce basic notions on coupled cell networks and their associated systems of admissible differential equations. Periodic states also possess spatio-temporal symmetries, leading to phase relations; these are classified by the *H*/*K* theorem and its analog for general networks. Systematic general methods for computing the stability of synchronous states exist for symmetric networks, but stability in general networks requires methods adapted to special classes of model equations. *Published by AIP Publishing.* [http://dx.doi.org/10.1063/1.4953664]

Networks describe how dynamical systems interact. A cell, or node, represents a component subsystem, and a connection represents an input from one cell to another. Applications are widespread; they include gene regulation networks, which organize the activity of genes in a developing organism; food webs, which describe the interactions between predators and their prey in an ecosystem; and neural networks, such as the brain. Networks often display patterns of synchrony, in which clusters of cells behave in the same manner. A related phenomenon, occurring when the system oscillates periodically, is phase-locking: cells behave the same way, except for a time delay. Coupled cell systems provide a general mathematical context for studying networks, applicable to many different real-world models; for example, animal locomotion and the visual system. Symmetry leads to patterns of synchrony, but other patterns may occur. The theory provides a classification, for any network, of all possible rigid patterns of synchrony and phase-locking: those that persist when the model equations are perturbed. It also provides methods for finding these patterns in a given model. A key feature is the notion of a balanced coloring, which provides consistent inputs to synchronous cells and classifies invariant synchrony subspaces. Stability of a synchronous state depends on eigenvalues of the Jacobian transverse to a synchrony subspace. Systematic methods to compute stabilities, based on irreducible representations, exist for symmetric networks. For general networks, only special types of model equation and network topologies (such as feedforward) are understood in detail.

I. INTRODUCTION, EXAMPLES, AND OVERVIEW

This paper discusses four separate but related issues: rigid patterns of synchrony for equilibria, rigid patterns of phase-shift synchrony for periodic cycles, stability of synchronous states, and the relation between these topics and network symmetry. We discuss these issues from the general viewpoint of coupled cell systems. This is a specific formal setting for network dynamics, focused on general features created by the network topology, rather than on more detailed features of specific models or classes of models. We survey some of the basic concepts and results in this area.

Roughly speaking, the *pattern of synchrony* associated to a state $x = (x_1, \ldots, x_n)$ in an n-cell network is a coloring of the n cells where two cells c, d have the same color only if $x_c = x_d$. The pattern of synchrony for an equilibrium is *rigid* if perturbing the network system moves the equilibrium, but does not change its pattern of synchrony. A T-periodic solution $x(t) = (x_1(t), \ldots, x_n(t))$ has phase-shift synchrony in cells c and d if

$$x_d(t) = x_c(t + \theta_{cd}T),$$

where $0 \le \theta_{cd} < 1$. The pattern of phase-shift synchrony for $x(t)$ is the set $\Theta = \{\theta_{cd}\}$. This pattern is *rigid* if perturbing the network system perturbs $x(t)$ but does not change Θ. This paper reviews the classification of rigid patterns and the subtle relationships with "balanced colorings" and "network symmetries."

Synchronous behavior in networks of dynamical systems (ordinary differential equations (ODE)) has been widely studied. It occurs when observations of distinct cells of the network lead to time series that closely resemble each other. The strongest form of resemblance occurs when the time series are identical; at the other extreme, they may be distinct but significantly correlated.

More generally, sets of cells can synchronize in *clusters*: here observations of cells in the same cluster give very similar time series, but time series from cells in distinct clusters differ. A partition into synchronous clusters is a *pattern of synchrony*; see, for example, Refs. 7–9, 36, 38, and 39. Another term is *partial synchrony*. These papers contain special cases of a general combinatorial theorem that characterizes patterns

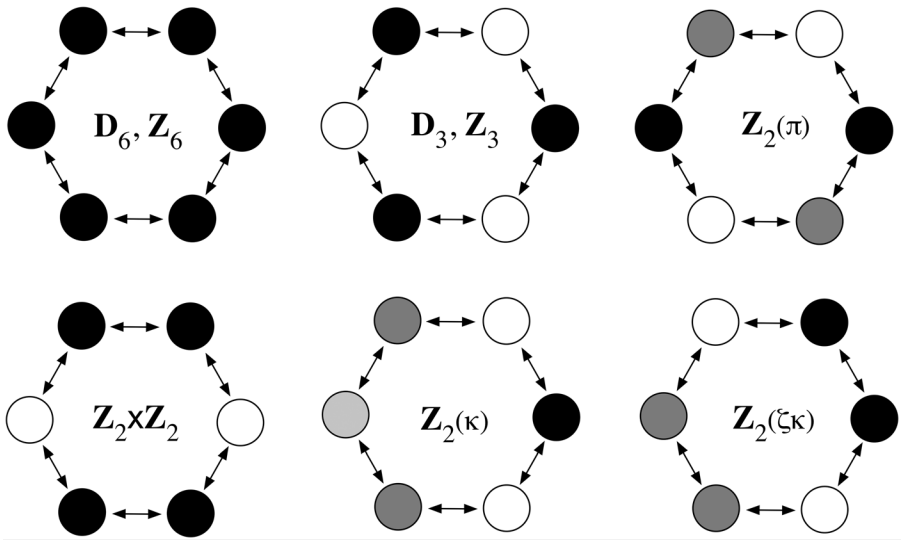

FIG. 1. Patterns of synchrony for equilibria in a 6-cell ring, induced by symmetry. The corresponding subgroup is indicated at the center of each ring. The trivial pattern (all cell states distinct) is not shown; it corresponds to the identity subgroup.

of synchrony. We motivate and state this theorem in Section II B in terms of "balanced colorings."

Here, we give an overview of a general formalism for network dynamics, *coupled cell systems*, developed over the past decade, and describe some of the insights it provides into patterns of synchrony. It is well known[20,36] that there is a close relationship between patterns of synchrony and network symmetries, because symmetry-breaking naturally creates patterns. More surprising is the occurrence of patterns of synchrony that have nothing to do with symmetry in the conventional group-theoretic sense.[24,27,42]

Applications of symmetric coupled cell systems include animal locomotion,[10,12,22,23,37] binocular rivalry,[13,15] and the vestibular system.[26,33] Applications of general coupled cell systems include binocular rivalry[14] and homeostasis.[21]

There are several reasons for developing such a theory. One is to organize and unify the analysis of network dynamics and typical behavior. Another is that in many applications, especially in biology and neuroscience, accurate equations or key parameters such as reaction rates are not known. It is therefore useful to consider the behavior of entire classes of models, to see what they have in common and how they differ. For example, the existence of a state with certain features is often generic, but its stability is usually sensitive to changes in the detailed model. General methods for *calculating* stabilities are the most we can hope for.

A. Motivating examples

We now give a series of examples to illustrate general phenomena that will be examined in greater generality later.

Example I.1.

A bidirectional ring of identical cells with identical couplings is symmetric under the dihedral group $\mathbb{D}_6$, the symmetry group of a hexagon. The methods of symmetric bifurcation theory[20,25] show that there are many typical patterns of synchrony, associated with subgroups of the symmetry group. Figure 1 shows the nontrivial types of pattern; we explain their derivation in Section III. Here, cells with the same color are in the same state, a convention we use throughout.

For simplicity, the network illustrated has nearest-neighbor coupling, but the same catalog of patterns occurs if longer-range couplings are permitted, provided they preserve the $\mathbb{D}_6$ symmetry.

Example I.2.

In periodic dynamics, there is a further related phenomenon: cell states may be *phase-locked*. They then have the same waveform, but with phase shifts. Figure 2 (left) shows a ring of three identical FitzHugh-Nagumo neurons with unidirectional coupling; Figure 2 (right) shows a typical periodic state in which all cells have the same waveform, but successive waves are phase-shifted by one third of a period, see Section III.

Example I.3.

Symmetry of the network is a common source of patterns of synchrony, but not the only one. For example, the network of Figure 3 has only trivial symmetry, but we prove in Section III that the synchrony pattern shown by the different colors can occur for both equilibria and periodic states. Moreover, for suitable ODEs, there exist periodic states in which cells of the three colors have the same waveform, but with phase shifts $0, \frac{1}{3}, \frac{2}{3}$ of the period, much as in Figure 2 (right).

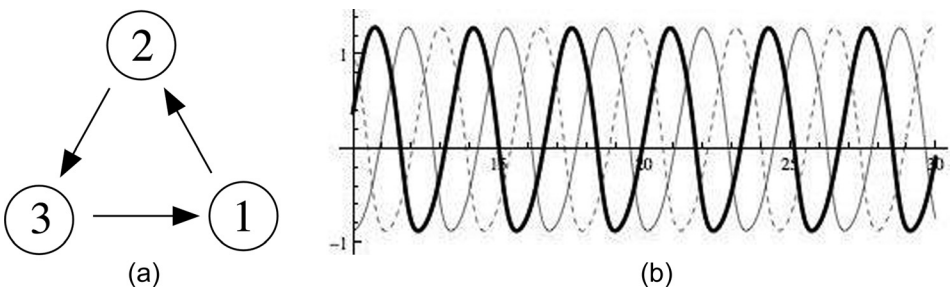

FIG. 2. *Left*: Ring of FitzHugh-Nagumo neurons with unidirectional coupling. *Right*: Periodic oscillations of the 3-cell ring exhibiting a $\frac{1}{3}$-period out of phase periodic solution. Time series show membrane potential in cells 1 (thick solid), 2 (thin solid), and 3 (dashed).

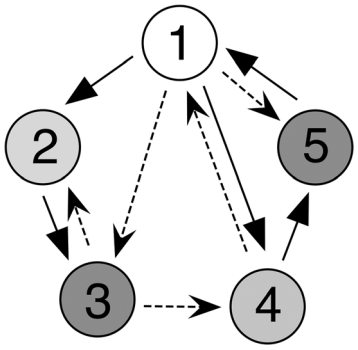

FIG. 3. Pattern of synchrony given by $x_2 = x_4$ and $x_3 = x_5$ in an asymmetric 5-cell network with two types of arrow.

B. Overview

Section II introduces the setting of coupled cell networks and admissible ODEs, explained informally using examples. The interplay between admissible maps and patterns of synchrony motivates the concept of a balanced coloring, and key properties are stated, in particular, the construction of a quotient network, in which synchronous cells are identified in a manner that preserves their dynamics.

Section III outlines fundamental ideas from symmetric dynamics, specializing them to symmetric networks. Subgroups of the symmetry group create natural invariant subspaces that induce patterns of synchrony. We discuss spatio-temporal symmetries of periodic states, and their relation to two distinct symmetry groups: spatial (pointwise) and spatio-temporal (setwise) symmetries. We state the *H*/*K* theorem for general ODEs, which classifies possible spatio-temporal symmetries. This theorem must be modified in the context of networks, and the results are different when the state spaces of cells are multidimensional $\mathbb{R}^k$, one-dimensional $\mathbb{R}$, or the circle $\mathbb{S}^1$ (phase oscillators). We discuss multirhythms, a type of resonance caused by symmetry. Generalizations to arbitrary networks are stated.

Section IV gives examples of anomalous patterns of synchrony and phase shifts, existing in symmetric networks but not caused by symmetry.

Section V discusses stability of a pattern of synchrony with respect to synchrony-breaking perturbations. We call this *transverse stability*, because it concerns the dynamics transverse to the synchrony subspace. It is best understood in the symmetric case; for general networks, it depends on specific model equations.

Section VI discusses general networks, where rigid patterns of synchrony—those preserved by small perturbations of the admissible ODE—correspond to balanced colorings, both for equilibria and periodic states. There is an analog of the *H*/*K* theorem for rigid patterns of phase shifts, which are induced by cyclic group symmetry on the quotient network defined by synchrony.

II. COUPLED CELL NETWORKS

First, we sketch the formalism of Refs. 27 and 42: coupled cell networks, with associated ODEs called coupled cell systems. Here, the *cells* (nodes) of the network correspond to state variables and the *arrows* (directed edges) indicate couplings. Each arrow has a *head* cell (to which it points) and a *tail* cell. A key feature is that arrows are classified into one or more *types*. Arrows of the same type couple their inputs to their outputs in the same manner. There is also a notion of cell type: roughly speaking, cells with the same state space have the same type.

Associated with each such network is a class of *admissible* ODEs: those that respect the network structure and the arrow types. We introduce these ODEs below.

Formal definitions can be found in Refs. 27 and 42, but here we work with typical examples, starting with Example I.3 (see Figure 3). Its *network diagram* has five cells and two types of arrow, shown with solid and dashed lines (and different arrowheads for emphasis). All cells have the same type and are drawn as circles.

Bidirectional arrows, as in Figure 1, should be interpreted as shorthand for two identical arrows, one in each direction.

A network is *path-connected* or *transitive* if any cell is connected to any other by some directed path (chain of arrows linked head to tail). It is *homogeneous* if all cells have the same number of input arrows of each type.

A. Admissible maps

We now associate with any network diagram a class of maps (or vector fields), said to be *admissible*, which respect the network topology and determine a class of ODEs coupled together according to the network.

The state (or phase) space P_c of each cell c can be any manifold; common choices are $\mathbb{R}^k$ for some k, especially $k = 1$, or the circle $\mathbb{S}^1$ for phase oscillators. For simplicity, assume $P_c = \mathbb{R}$. Assign a state variable $x_c \in \mathbb{R}$ to each cell c. By convention, the time-derivative $\dot{x}_c$ is some function of x_c, together with the tail cells x_d of all arrows with head c. For example, cell 4 receives inputs from cells 1 (solid arrow) and 3 (dashed arrow). Therefore, the corresponding component of a system of admissible ODEs takes the form

$$\dot{x}_4 = f(x_4, x_1, x_3), \tag{2.1}$$

for an arbitrary (infinitely differentiable) function f. By convention, the internal state variable x_4 is written first.

Now consider another cell, say 1. This has internal variable x_1, and receives inputs from cells 4 (dashed arrow) and 5 (solid arrow). Therefore, cell 1 has the same *input type* as cell 4: there is a one-to-one correspondence between the sets of all input arrows that preserves arrow type. In the formalism, this correspondence implies that the equation for $\dot{x}_1$ involves the same function f, with variables inserted in a manner that preserves arrow types. That is,

$$\dot{x}_1 = f(x_1, x_5, x_4)$$

with variables in the same order: internal, solid arrow, dashed arrow.

In this example, all five cells have the same input type (one solid arrow, one dashed), so the same f occurs for them all. The resulting system of ODEs is

$$\begin{aligned}\dot{x}_1 &= f(x_1, x_5, x_4),\\ \dot{x}_2 &= f(x_2, x_1, x_3),\\ \dot{x}_3 &= f(x_3, x_2, x_1),\\ \dot{x}_4 &= f(x_4, x_1, x_3),\\ \dot{x}_5 &= f(x_5, x_4, x_1).\end{aligned}$$

The map $F : \mathbb{R}^5 \to \mathbb{R}^5$ whose components are these five functions defines a vector field on $\mathbb{R}^5$. We call F an *admissible vector field*, or more briefly *admissible map*, for the given network. The associated system of ODEs is an *admissible ODE*.

The general recipe that associates to any network diagram a class of admissible maps works in exactly the same way. Choose a state space P_c for each cell c, with state variable $x_c \in P_c$. Use the set of input arrows to c to define a component $\dot{x}_c = f_c(x_c, x_{T(c)})$ of a system of ODEs, where $x_{T(c)}$ is the vector of state variables for the tail cells of the input arrows. If cells c, d have the same input type, require f_d to be equal to f_c, provided the input variables are arranged so that arrows of the same type correspond. These equalities of functions imply various equalities among the cell state spaces P_c, induced by input-equivalences. Cells with the same state space are said to have the same *cell type*.

Suppose that cell c receives two input arrows of the same type, with tail cells i, j. The recipe for inserting variables into f_c can lead equally well to either

$$f_c(x_c, \ldots, x_i, x_j, \ldots) \quad \text{or} \quad f_c(x_c, \ldots, x_j, x_i, \ldots).$$

To resolve this ambiguity, we require both of the above expressions to be equal. That is: if c has two (or more) inputs of the same arrow type, f_c is symmetric in the corresponding input variables. This is often shown by putting a bar over the variables concerned. For example, the bidirectional ring of Figure 1 has admissible ODEs of the form

$$\dot{x}_c = f_c(x_c, \overline{x_{c-1}, x_{c+1}})$$

with subscripts taken (mod 6).

Three further features should be noted:

(1) Arrows can form *self-loops* with the same head and tail cell.
(2) Several arrows may have the same head and the same tail.
(3) The state variable x_c of each cell c is assumed to appear as a distinguished variable in the corresponding f_c. If there are self-loops, it may appear elsewhere too.

We refer to these conventions as the *multiarrow formalism*. Although multiple arrows and self-loops may appear artificial, this convention can be motivated both by applications and by the internal requirements of the theory.[27] Convention (3) was originally assumed for pragmatic reasons: it makes bifurcation theory simpler because the identity map is admissible.

Remark II.1.

In this set-up, individual arrows do not correspond to specific *terms* in the ODE. This differs from other approaches, such as networks of nonlinear oscillators with linear coupling,[32,36] where (2.1) would be replaced by

$$\dot{x}_4 = f(x_4) + ax_1 + bx_3.$$

Instead, arrows specify which *variables* occur (perhaps nonlinearly) in which components of the ODE, and encode (via input sets of arrows) when components of the ODE involve the same function. They also encode symmetries of those functions, induced by permuting input arrows of the same type.

Special assumptions about the form of F are consistent with the coupled cell formalism, but introduce extra structure that may impose extra constraints on the dynamics.

B. Synchrony and balanced colorings

Throughout this paper, we employ a strong notion of synchrony: time-series are identical. Weaker notions of synchrony can also be considered in the coupled cell formalism, but we focus here only on the stronger notion.

Definition II.2.

Let $x(t)$ be a solution of an admissible ODE. Cells c, d are *synchronous* on $x(t)$ if

$$x_c(t) \equiv x_d(t) \quad \forall t \in \mathbb{R}.$$

A *pattern of synchrony* is a partition of the cells into disjoint subsets, such that cells are synchronous on $x(t)$ if and only if they belong to the same part. (Alternatively, the pattern of synchrony is the equivalence relation corresponding to the partition.) For example, in Figure 3 the pattern of synchrony is $\{1\}, \{2,4\}, \{3,5\}$.

Diagrammatically, a pattern of synchrony is often represented by coloring the cells so that synchronous cells have the same color.

We now explain why the pattern of synchrony in Figure 3 is natural and typical. Suppose it occurs for some solution $x(t)$ of the admissible ODE. Then we must have

$$x_2(t) \equiv x_4(t) \quad x_3(t) \equiv x_5(t) \quad \forall t \in \mathbb{R}.$$

Let $y_1 = x_1, y_2 = x_2 = x_4, y_3 = x_3 = x_5$, and substitute to obtain the *restricted* ODE

$$\begin{aligned}\dot{y}_1 &= f(y_1, y_3, y_2),\\ \dot{y}_2 &= f(y_2, y_1, y_3),\\ \dot{y}_3 &= f(y_3, y_2, y_1),\\ \dot{y}_2 &= f(y_2, y_1, y_3),\\ \dot{y}_3 &= f(y_3, y_2, y_1).\end{aligned} \tag{2.2}$$

This system appears overdetermined (five equations in three unknowns). However, the two equations for $\dot{y}_2$ are identical, and so are those for $\dot{y}_3$. So we are left with a well-defined *reduced system*

$$\begin{aligned}\dot{y}_1 &= f(y_1, y_3, y_2),\\ \dot{y}_2 &= f(y_2, y_1, y_3),\\ \dot{y}_3 &= f(y_3, y_2, y_1).\end{aligned} \tag{2.3}$$

Any solution $y(t) = (y_1(t), y_2(t), y_3(t))$ of the reduced system can be *lifted* to yield a solution

$$x(t) = (x_1(t), x_2(t), x_3(t), x_2(t), x_3(t))$$

of the original ODE, and this has the pattern of synchrony {1}, {2, 4}, {3, 5}. This is the sense in which that pattern of synchrony is natural and typical.

The corresponding *synchrony subspace*

$$\Delta = \{x \in \mathbb{R}^5 : x_2 = x_4, x_3 = x_5\}$$

is an invariant subspace for *any* admissible map F; that is, $F(\Delta) \subseteq \Delta$. The reduced equation is defined by the restriction of F to Δ, projected onto $\mathbb{R}^3$ by mapping $(x_1, x_2, x_3, x_4, x_5)$ to (x_1, x_2, x_3). (We renamed this as (y_1, y_2, y_3) for clarity.)

Self-consistency of the restricted ODE, hence existence of the reduced ODE, is not automatic for an arbitrary pattern of synchrony. For example, suppose we instead work with the partition {1, 2}, {3}, {4, 5}. The first two components of the restricted ODE (2.2) become

$$\begin{aligned} \dot{y}_1 &= f(y_1, y_4, y_4) \\ \dot{y}_1 &= f(y_1, y_1, y_3) \end{aligned}$$

which are contradictory.

In Ref. 42, extended to the multiarrow formalism in Ref. 27, it is proved that the following are equivalent:

(1) The restricted ODE is consistent, so the reduced ODE is well-defined, for all admissible F.
(2) The synchrony space Δ is invariant under all admissible F.
(3) The pattern of synchrony is a *balanced coloring*. That is, if cells c, d have the same color, their input sets correspond in a manner that preserves arrow types *and* assigns the same colors to corresponding tail cells.

This theorem classifies all possible patterns of synchrony that are *robust*—common to all admissible maps. Each pattern exists in any network, for any "generic" admissible map: solve the reduced ODE and lift.

The underlying intuition here is as follows. Suppose that, by any sensible definition of synchrony, a pattern of synchrony occurs that is not "accidental," that is, does not depend on very special choices of the admissible map. Then corresponding input cells of synchronous cells, compared in suitable pairs, are themselves synchronous. More succinctly: *synchronous cells have synchronous input patterns*. If not, differences in inputs would push them away from synchrony. This intuition is good motivation, but it is insufficient to prove theorems about patterns of synchrony.

In Sections III and VI, we show that balanced colorings also classify typical patterns of synchrony for equilibria and for periodic states, where "typical" means that the patterns are structurally stable. That is, they persist if F is perturbed slightly (while remaining admissible).

Algorithms to compute balanced colorings have been devised.[1,30] Balanced colorings are essentially the same as clusters,[8,9,36] and many existence results in the literature can be explained in a unified manner using balanced colorings. In Ref. 7, it is observed that invariant subspaces may be nested inside each other, leading to hierarchies of such subspaces. In general, this behavior is characterized by the lattice of invariant subspaces, which is dual to the lattice of balanced colorings.[40]

C. Quotient networks

As f varies over all functions, the reduced system (2.3) gives precisely the admissible ODEs for another network, with three cells (one for each color), as in Figure 4.

To form this 3-cell network, take one cell of each color. For each of these cells, copy its input set from the original network, matching all colors of tail cells. Balance is precisely the condition that this can be done consistently.

This construction, the formation of a *quotient network*, is valid for any balanced coloring. The admissible maps for the quotient network are precisely the restrictions to the corresponding synchrony subspace of admissible maps for the original network. Conversely, any admissible map on the quotient network is the reduced map for an admissible map on the original network—it can be *lifted*. Again, these results are proved in Refs. 27 and 42.

The term "quotient" is used here because the network diagram is obtained by identifying cells and copying input sets. This is a quotient by an equivalence relation. The reduced maps are *restrictions* of the original maps—more precisely, projections of restrictions in which redundant coordinates are removed.

III. SYMMETRY

Patterns of synchrony arise naturally when the network has symmetry. In this section, we establish some basic results and give illustrative examples. We consider both equilibria and periodic states, and describe patterns of phase shifts as well as synchrony.

A. Equivariant ODEs

Before specializing to networks, we recall some basic concepts from symmetric ("equivariant") dynamics.[20,25] Let Γ be a finite group acting linearly on a finite-dimensional vector space V. A map $F : V \to V$ is Γ-*equivariant* if

$$F(\gamma x) = \gamma F(x) \quad \forall x \in V.$$

Consider the corresponding equivariant ODE

$$\frac{dx}{dt} = F(x). \tag{3.1}$$

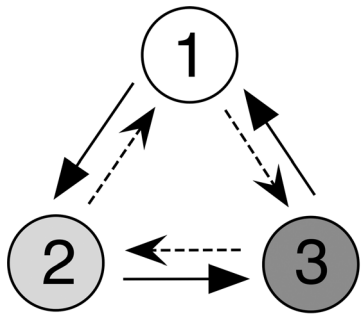

FIG. 4. Quotient network for the pattern of synchrony in Figure 3.

If $x(t)$ is a solution, so is $\gamma x(t)$ for any $\gamma \in \Gamma$

$$\frac{\mathrm{d}}{\mathrm{d}t}\gamma x(t) = \gamma \frac{\mathrm{d}}{\mathrm{d}t}x(t) = \gamma F(x(t)) = F(\gamma x(t)). \qquad (3.2)$$

Recall that an *orbit* of Γ on V is a set of the form $\{\gamma v_0 : \gamma \in \Gamma\}$ for some choice of v_0. In this language, Equation (3.2) states that solutions occur as group orbits. Conversely, this property of solutions implies equivariance of F.

Let $x(t) \equiv x_0$ be an equilibrium. Then γx_0 is also an equilibrium, but need not equal x_0. We therefore define the *isotropy subgroup* of x_0 to be

$$\Gamma_{x_0} = \{\gamma \in \Gamma : \gamma x_0 = x_0\}.$$

This is the symmetry group of x_0. We say that x_0 *breaks symmetry* from Γ to Γ_{x_0}. Conversely, given a subgroup $\Sigma \subseteq \Gamma$, we define its *fixed-point subspace* to be

$$\mathrm{Fix}(\Sigma) = \{x : \sigma x = x \, \forall \sigma \in \Sigma\}.$$

More generally, we can define the isotropy subgroup of a solution $x(t)$ to be

$$\Gamma_{x(t)} = \{\gamma \in \Gamma : \gamma x(t) = x(t) \, \forall t \in \mathbb{R}\}.$$

A basic result is:

Theorem III.1.

For any subgroup $\Sigma \subseteq \Gamma$, the space $\mathrm{Fix}(\Sigma)$ is invariant under F.

Proof. Let $x \in \mathrm{Fix}(\Sigma)$, and let $\sigma \in \Sigma$. Then

$$\sigma F(x) = F(\sigma x) = F(x)$$

so $F(x) \in \mathrm{Fix}(\Sigma)$. □

Although the proof is trivial, the result provides a method for finding solutions $x(t)$ of the ODE that break symmetry to any given Σ. Namely: *restrict* the ODE to $\mathrm{Fix}(\Sigma)$ and solve. Usually $\mathrm{Fix}(\Sigma)$ is smaller than V, a bonus.

Solutions found by this method need not be asymptotically stable. Symmetry methods can be employed to simplify stability computations, but stability is a separate issue, addressed in Section V.

B. Network symmetries

We now specialize the equivariant theory to symmetric networks. Most of the equivariant results still apply when the system is admissible for a Γ-symmetric network, where now Γ is a permutation group acting on the cells. In a symmetric network, all admissible maps are equivariant, but equivariant maps need not be admissible because admissible maps satisfy extra constraints.[3,4]

The *symmetry group* of a network is the group Γ of all permutations γ of its cells that preserve the arrows, in the sense that for any pair of cells c, d the number of arrows from c to d of a given type is the same as the corresponding number for arrows from $\gamma(c)$ to $\gamma(d)$.

Orbits for permutation actions are defined to be sets of the form $\{\gamma(c) : \gamma \in \Gamma\}$ for some choice of cell c. The orbits partition the set of cells. The permutation action of Γ on cells induces an action on state variables by $x_c \mapsto x_{\gamma^{-1}(c)}$.

Theorem III.2.

Consider a network with symmetry group Γ, and any subgroup $\Sigma \subseteq \Gamma$. Then a solution $x(t)$ that lies in Fix(Σ) has the pattern of synchrony determined by the orbits on Σ on cells.

Proof. If $c \in \mathrm{Fix}(\Sigma)$ then $c = \sigma(c)$ for all $\sigma \in \Sigma$, hence also $c = \sigma^{-1}(c)$ since also $\sigma^{-1} \in \Sigma$. Thus

$$x_{\sigma(c)}(t) \equiv x_c(t) \quad \forall t \in \mathbb{R}$$

so $x(t)$ is synchronous on each orbit of Σ. □

Such a pattern is automatically balanced, but this can also be proved directly.

Figure 1 is an example. The choice of Σ is shown at the center of each picture, and the corresponding pattern of synchrony is shown by shading synchronous cells identically. The notation for the subgroups is determined by

$$\pi = (14)(25)(36),$$
$$\kappa = (26)(34),$$
$$\zeta = (123456).$$

Generators are included in parentheses (for example, $\mathbb{Z}_2(\pi)$) where the conjugacy class of the subgroup is ambiguous; otherwise the symbol indicates the isomorphism type of the subgroup. For example, $\mathbb{Z}_3$ is the cyclic subgroup of order 3 generated by ζ^2. Notice that different subgroups may generate the same pattern.

C. Spatio-temporal symmetries

The above method applies to synchronous solutions of any type: equilibrium, periodic, even chaotic. But it addresses only spatial (pointwise) symmetries of the solution: those valid for all time. Periodic states also have *temporal* symmetries; for example, by definition a periodic state is symmetric under phase shifts that are integer multiples of the period. Combining the two leads to *spatio-temporal* symmetries, which are fundamental for periodic states.

Example III.3. We discuss Example I.2 in more detail. The time series in Figure 2 (right) are generated by a model in which each cell is a FitzHugh-Nagumo neuron, with voltage-coupling. Let v_i denote the membrane potential of cell i, let w_i be a surrogate for an ionic current, and suppose that a, b, γ are parameters with $0 < a < 1$, $b > 0, \gamma > 0$. The coupling adds a voltage term to each cell equation, giving the system

$$\begin{aligned} \dot{v}_1 &= v_1(a - v_1)(v_1 - 1) - w_1 - cv_2 & \dot{w}_1 &= bv_1 - \gamma w_1 \\ \dot{v}_2 &= v_2(a - v_2)(v_2 - 1) - w_2 - cv_3 & \dot{w}_2 &= bv_2 - \gamma w_2 \\ \dot{v}_3 &= v_3(a - v_3)(v_3 - 1) - w_3 - cv_1 & \dot{w}_3 &= bv_3 - \gamma w_3. \end{aligned} \qquad (3.3)$$

The symmetry group of the network is the cyclic group $\mathbb{Z}_3$ generated by the 3-cycle (123), acting on pairs (v_j, w_j) by permuting the indices cyclically.

When $a = b = \gamma = 0.5$ and $c = 0.8$, a numerical simulation shows that the origin is a stable equilibrium for the full six-dimensional system. In this state, the cells are synchronous. In contrast, when $a = b = \gamma = 0.5$ and $c = 2$, the

system has no stable equilibrium (synchronous or not). Instead, it is attracted to a stable periodic state in which successive cells are one third of a period out of phase, Figure 2 (right). This figure shows the pattern for the v_j; a similarly phase-locked pattern occurs for the w_j. Such a pattern is called a *discrete rotating wave*,[25] *phase-shift synchrony*,[20] or *rosette phase locking*.[28]

This periodic state has spatio-temporal symmetry. If the period is T, and we set $x(t) = (v(t), w(t))$, it satisfies the phase relationships

$$x_2(t) = x_1(t - T/3) \quad x_3(t) = x_1(t - 2T/3)$$

and the solution $x(t)$ is invariant if we permute the labels using the 3-cycle $\rho = (123)$ and shift phase by $T/3$. That is,

$$\rho x(t + T/3) = x(t).$$

Thus $x(t)$ is fixed by the element $(\rho, T/3) \in \Gamma \times \mathbb{S}^1$, where $\mathbb{S}^1$ is the circle group of phase shifts modulo the period.[25]

D. Pointwise and setwise symmetries

Spatio-temporal symmetries can be defined in a similar manner for periodic states of any symmetric dynamical system; in particular, any admissible ODE for a symmetric network. However, there is an alternative approach, which generalizes to chaotic states too—indeed, to states given by any dynamical attractor, in any reasonable sense of that term.

Associated with any attractor A are two subgroups of Γ, its setwise and pointwise symmetries

$$H_A = \{\gamma \in \Gamma : \gamma A = A\}$$
$$K_A = \{\gamma \in \Gamma : \gamma|_A = \mathrm{id}\}.$$

Clearly $K_A \triangleleft H_A$, so the quotient group H_A/K_A is defined.

If A is an equilibrium then it is a single point, so $H_A = K_A = \Sigma_A$ and $H_A/K_A = 1$. An obvious necessary and sufficient condition for a given H_A to occur is that it should be an isotropy subgroup of Γ.

If A is a periodic cycle, the quotient group H_A/K_A can be identified with phase shifts. To see how, suppose that $x(t)$ is a solution of the ODE defining the periodic cycle. If $\gamma \in H_A$ then $\gamma x(t)$ is also a solution. But γ fixes A setwise, so $\{\gamma x(t) : t \in \mathbb{R}\} = \{x(t) : t \in \mathbb{R}\}$. There exists $\phi \in \mathbb{S}^1$ such that $\gamma x(0) = x(\phi)$. Now

$$\gamma x(t - \phi) = x(t) \quad \forall t \in \mathbb{R}$$

because both sides satisfy the same ODE and have the same initial condition at $t = \phi$, so by uniqueness of solutions of ODEs they are identical. But this equation determines a spatio-temporal symmetry. Since K_A acts trivially, the action of H_A factors through K_A giving an action of H_A/K_A. If H_A is finite (as it must be for networks) then H_A/K_A is a finite subgroup of $\mathbb{S}^1$, hence a cyclic group $\mathbb{Z}_k$ for some k.

Example III.4.

In Example I.2 $H_A = \mathbb{Z}_3$ and $K_A = 1$. Let $v(t)$ be a T-periodic solution to (3.3) and that $\rho = (123)$ generates the group $H_A \cong \mathbb{Z}_3$. Then $\rho v(t)$ is also a periodic trajectory, differing only by time-translation. That is, $\rho v(t) = v(t + \theta)$ for all t. Applying the permutation $\rho = (123)$ three times (which gives the identity) implies that $3\theta \equiv 0 (\mathrm{mod}\, T)$. Hence either $\theta = 0, \frac{T}{3}, \frac{2T}{3}$. But $\theta \neq 0$ by assumption. The other two yield rotating waves, which travel in opposite directions in the sense that $\frac{2T}{3} = -\frac{T}{3}$ modulo T.

Figure 5 shows the trajectory of $v(t)$ in $\mathbb{R}^3$, viewed from a point very close to the main diagonal. The periodic cycle is shaped like a curved equilateral triangle, revealing the setwise $\mathbb{Z}_3$ symmetry.

An important feature of symmetry-induced phase shifts in periodic states is *rigidity*: if the vector field is slightly perturbed by an equivariant perturbation, the phase shifts remain unchanged (as a fraction of the period).[20] Rigidity is not typical of phase shifts in general dynamical systems.

E. *H*/*K* theorem

A *pattern of phase shifts* is similar to a pattern of synchrony, but phases are also taken into account. Cells whose states are phase-related with phase difference 0 (that is, cells in the same K_A-orbit) are synchronous. But other pairs of cells (those in the same H_A-orbit but not in the same K_A-orbit) have the same waveform but different phases. We do not formalize this notion here. The pair (H_A, K_A) determines the pattern of phase shifts, up to a slight ambiguity in the assignment of a phase to a generator of the group. So it is natural to ask for a classification of the possible pairs (H_A, K_A).

For general dynamical systems, this is provided by the H/K theorem of Ref. 11. Let $N_\Gamma(K)$ denote the normalizer of K in Γ, let Γ_x denote the isotropy subgroup of $x \in \mathbb{R}^N$, and define a subset of $\mathbb{R}^N$ by

$$L_K = \bigcup_{\gamma \notin K} \mathrm{Fix}(\gamma) \cap \mathrm{Fix}(K) = \{x \in \mathrm{Fix}(K) : K \subsetneq \Gamma_x\}.$$

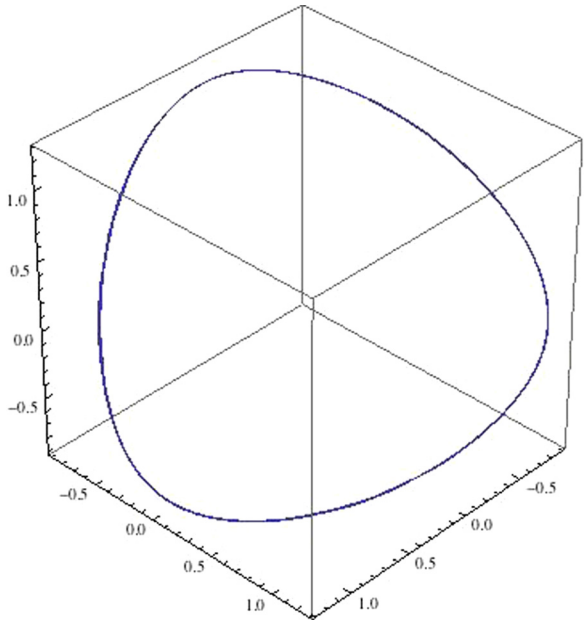

FIG. 5. Setwise $\mathbb{Z}_3$ symmetry of periodic trajectory of three coupled Fitzhugh-Nagumo neurons.

FIG. 6. 3-cell network supporting a multirhythm state.

Theorem III.5. *Let* Γ *be a finite group acting on* $\mathbb{R}^N$ *and let* $H \supseteq K$ *be subgroups of* Γ. *There exists a hyperbolic periodic solution for a* Γ*-equivariant vector field on* $\mathbb{R}^N$ *with spatial symmetries* K *and spatiotemporal symmetries* H *if and only if*

(a) K *is a normal subgroup of* H *and* H/K *is cyclic*.
(b) K *is an isotropy subgroup of* Γ.
(c) $\mathrm{dimFix}(K) \geq 2$, *and if* $\mathrm{dimFix}(K) = 2$ *then either* $H = K$ *or* $H = N_\Gamma(K)$.
(d) H *fixes a connected component of* $\mathrm{Fix}(K) \backslash L_K$.

Part (d) arises because of certain geometric obstacles associated with L_K. The proof shows that in the "if" part of the theorem, which asserts the existence of suitable periodic states, the periodic state concerned can be made asymptotically stable. This theorem does not assert that periodic states with given H, K occur for any admissible map, which is obviously false. It provides a complete catalog of the combinations that exist for *some* admissible map.

Analogs of this theorem for symmetric networks are examined in Ref. 17, for three distinct cases, in which cell state spaces are: $\mathbb{R}^k$ for any k (coupled systems); $\mathbb{R}$ (coupled equations); $\mathbb{S}^1$ (coupled oscillators). The key point is that *these classifications are different*. In other words, the state spaces of cells affect which patterns of phase shifts are possible. The results can be summarized as follows:

Systems: (a, b) as above. Change (c) to "if $\mathrm{dimFix}(K) = 2$ then $H = K = \Gamma$."
Equations: (a, b, d) as above. Change (c) to "$\mathrm{dimFix}(K) \geq 2$, and if $\mathrm{dimFix}(K) = 2$ then $H = K$."
Oscillators: (a, b, d) as above. Change (c) to "if $\mathrm{dimFix}(K) = 2$ then $H = K = \Gamma$; if $\mathrm{dimFix}(K) = 2$ then either $H = K$ or $H = N_\Gamma(K)$ and $N_\Gamma(K) \cong \mathbb{Z}_2$."

These differences have two causes. Network symmetry groups are permutation groups, with special features, and the topology of cell state spaces imposes geometric constraints. Again the proofs show that in the "if" part of the theorem the periodic state concerned can be made asymptotically stable. A similar classification for coupled systems given by path-connected networks was proved earlier.[29]

F. Multirhythms

Symmetry can sometimes force a kind of resonance, in which some cells oscillate with a frequency that is a rational multiple of that of other cells. The overall state is periodic, but individual cells have different periods. A simple example arises for the three-cell network of Figure 6. This has $\mathbb{Z}_2$ symmetry, generated by $\sigma = (13)$ which fixes cell 2. By the H/K Theorem there can be a periodic state with $H = \mathbb{Z}_2, K = 1$. This has spatio-temporal symmetry generated by $(\sigma, T/2) \in \mathbb{Z} + 2 \times \mathbb{S}^1$: that is, swap cells using σ and shift phase by half a period. This symmetry requires cells 1 and 3 to be half a period out of phase with each other; but because cell 2 is fixed, symmetry requires it to be half a period out of phase with *itself*. Therefore, such states have the form

$$(x(t), y(t), x(t + T/2)) \quad y(t) = y(t + T/2)$$

implying that cell 2 oscillates with twice the frequency of cells 1 and 3. Such states can be found in simulations: we call them *multirhythms*. Unlike standard resonances, they arise because of symmetry. More elaborate examples are given in Ref. 20, showing in particular, that it is possible for the minimal period of every cell to differ from that of the system as a whole; this occurs, for example, when symmetry leads to a 2:3 resonance.

IV. ANOMALOUS PATTERNS

When a network has symmetry, it is easy to imagine that its behavior is typical of symmetric dynamical systems with the same symmetry group. In fact, this assumption is often incorrect. If so, we call the behavior concerned *anomalous*. The reason is that although admissible maps are always equivariant, the converse can be false. In particular, equivariant maps need not depend on the correct input cells. Even when this restriction is added, admissible maps may obey extra constraints.

Figure 7 is a case in point. It has three cells, and is homogeneous, with each cell receiving two inputs. (It is not path-connected, but that can be remedied by adding more arrows and the results do not change significantly.) The figure shows three 2-colorings. Each is balanced, and the corresponding quotient network is shown below the original.

The 3-cell network has $\mathbb{Z}_2$ symmetry, given by the permutation (12). The only nontrivial (not all identical or all different) pattern of synchrony predicted by the symmetry group is {1, 2}, {3} as in (a). However, there are two more:

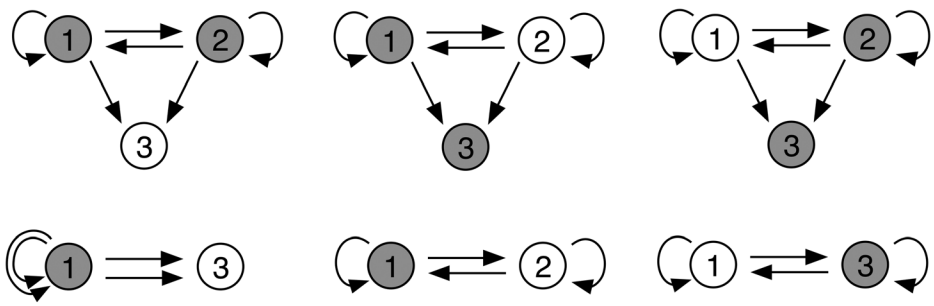

FIG. 7. Patterns of synchrony induced by symmetry (a) and by anomalous balanced colorings (b) and (c).

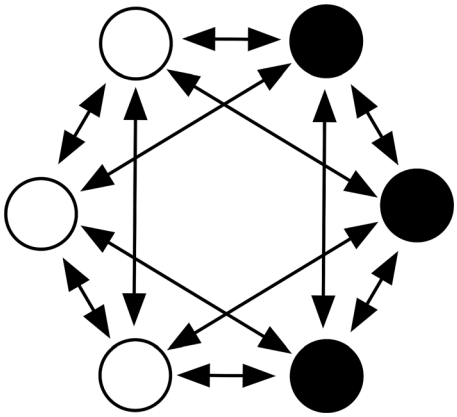

FIG. 8. 6-cell network with a balanced coloring not determined by symmetry.

{1, 3}, {2} (b) and {1}, {2, 3} (c). (To check balance in these two case, note that each grey cell receives one grey and one white input, and so does each white cell.) In case (a) the quotient is asymmetric. Both (b) and (c) have quotient networks with $\mathbb{Z}_2$ symmetry.

Consider periodic states, and to avoid dimension restrictions in the *H*/*K* theorem assume all cell phase spaces have dimension ≥ 2. By the *H*/*K* theorem, the $\mathbb{Z}_2$ symmetry of the original network predicts a synchronized state of the form

$$(x(t), x(t), y(t))$$

and a multirhythm state of the form

$$(x(t), x(t+T/2), y(t)) \text{ where } y(t+T/2) = y(t).$$

For the pattern of synchrony (b), the $\mathbb{Z}_2$ symmetry of the quotient predicts periodic states of the forms

$$(x(t), x(t), x(t)) \quad (x(t), y(t), x(t)) \quad (x(t), x(t+T/2), x(t)).$$

In the third state, cells 1 and 2 are half a period out of phase; but instead of cell 3 having twice the frequency, it is synchronous with cell 1.

Pattern (c) gives similar results but with cells 1 and 2 interchanged.

Example IV.1.

A pattern of synchrony in a symmetric network, not given by the orbits of a subgroup, is shown in Figure 8, and was discussed in Ref. 24. Here, the longer range arrows have the same type as the short range ones.

Example IV.2.

Example IV.1, although a valid network, is slightly artificial because arrows unrelated by the symmetry group are given the same type. Figure 9 shows a pattern of synchrony on a 64-cell network, defined on a square lattice (mod 8). The symmetry group Γ is generated by translation in both directions and the symmetries of the square. The figure shows only nearest-neighbor connections. However, if these are supplemented by longer-range connections, in any manner, subject only to the condition that all arrows in the same Γ-orbit are included and have the same arrow-type, the pattern shown is balanced but is not the fixed-point set of a subgroup of Γ.[3,4]

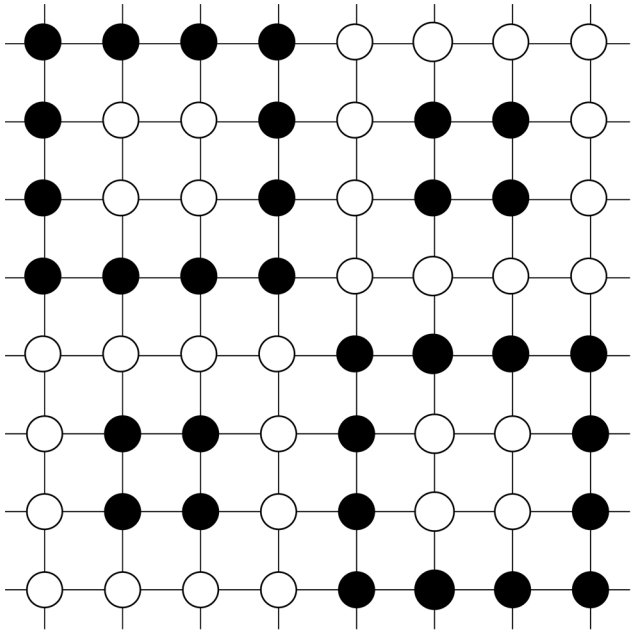

FIG. 9. 64-cell network with a balanced coloring not determined by symmetry, even when extra group orbits of arrows are added. Arrows omitted; figure wraps round onto a torus.

Example IV.3.

The $\mathbb{Z}_3$ symmetry of the left-hand network of Figure 10 predicts, via the *H*/*K* Theorem, a rotating wave multirhythm of the form

$$(x(t), x(t+T/3), x(t+2T/3), y(t)), \tag{4.1}$$

where $y(t)$ has triple the frequency of $x(t)$. On the other hand, the 2-cell quotient predicts a pattern of the form

$$(x(t), x(t+T/2), x(t+T/2), x(t+T/2)). \tag{4.2}$$

Both are possible with suitable state space dimensions and initial conditions. But only the first is evident from the symmetry of the left-hand network.

Recently, Pecora *et al.*[36] studied a special space of admissible systems for a special class of networks with one

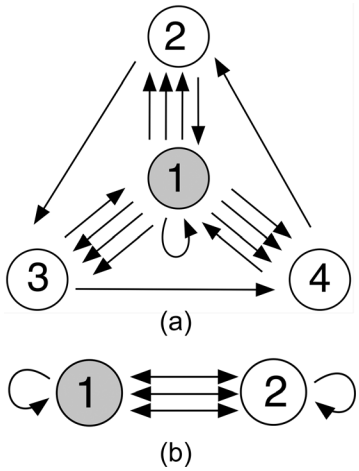

FIG. 10. *Left*: Multiarrow network with $\mathbb{Z}_3$ symmetry. *Right*: Quotient with $\mathbb{Z}_2$ symmetry.

type of node and one type of bidirectional coupling. Examples IV.1 and IV.2 fall into their class and show that even in this restricted case there can exist clustering forced by balanced colorings but not forced by symmetry. Their extensive calculations on many natural and randomly generated networks were done using discrete algebra software and show that many networks have clustering forced by symmetry.

V. STABILITY

In applications, an important issue is not just the existence of a state of some particular type, but its stability.[7,20,25,38]

In symmetric systems, there is an extensive interplay between symmetry and stability, because symmetry imposes strong constraints on the structure of the Jacobian matrix, which can be exploited in calculations.[25] In the absence of symmetry, the network topology still constrains stability, but the relationship is complicated and results are less systematic. The theory for bifurcations, which describe what happens when a state loses stability, is in some respects more satisfactory, because loss of stability is assumed as a hypothesis; the theory focuses on the implications of this assumption rather than the conditions under which it is valid.

A. Transverse stability

We begin with generalities about the stability of a pattern of synchrony (or partially synchronous state), which splits the cells into synchronized clusters.

Consider an admissible ODE

$$\frac{\mathrm{d}x}{\mathrm{d}t} = F(x) \tag{5.1}$$

for some network. Suppose that $x(t)$ has some pattern of synchrony. Here, $x(t)$ can have any kind of dynamics, such as equilibrium, periodic, or chaotic. Equivalently, $x(t) \in \Delta$ where Δ is the corresponding synchrony subspace. Assume Δ is defined by a balanced coloring, as justified in Section II B and Theorems VI.3 and VI.4.

Then Δ is invariant under any admissible ODE; in particular, it is an invariant subspace for any specific model consistent with the network topology. Moreover, $x(t)$ is a solution of the reduced system on Δ.

Stability of $x(t)$ therefore decomposes into two components: the dynamics on Δ and that transverse to Δ. Stability on Δ is determined by the stability of $x(t)$ relative to the reduced system of ODEs $\frac{\mathrm{d}y}{\mathrm{d}t} = G(y)$, whose variables represent clusters. (For chaotic states, we interpret "stable" as: the closure of $x(t)$ is an *attractor* of the reduced system.) Intuitively, stability for G is about the effect of *synchrony-preserving* perturbations.

More interesting, and important in applications, is stability transverse to Δ. This corresponds to stability under *synchrony-breaking* perturbations, which change both the dynamics and the pattern of synchrony. The issues here are more complex, especially in the chaotic case. Moreover, we must distinguish between the transverse stability of Δ itself (all transverse eigenvalues have negative real part at every point of Δ) and the transverse stability of a given state $x(t)$ (all transverse eigenvalues have negative real part at every point $x(t)$).

For example, consider an equilibrium $u \in \Delta$. This is (linearly) stable if all eigenvalues of the Jacobian $DF|_u$ have negative real parts. Because Δ is invariant, $DF|_u$ also leaves Δ invariant. Therefore, its eigenvalues decompose into two sets: those whose eigenvectors lie in Δ, and the others ("transverse eigenvalues"). The problem is therefore to compute these eigenvalues.

B. Stability in symmetric networks

For symmetric networks, there is a systematic theory based on the representation of the symmetry group Γ on phase space, derived in detail in Ref. 25 for compact Lie groups (in particular, finite ones, the main case relevant to networks). This theory applies when $\Delta = \mathrm{Fix}(\Sigma)$ for a subgroup Σ. Section III explains its implications for the existence of specific patterns of synchrony. We sketch how the same framework can be used to analyse stability.

By Theorems III.1 and III.2, such a subspace is invariant and is given by a balanced coloring (the Σ-orbits). (However, it is worth noting that symmetric networks may have balanced colorings, hence invariant subspaces that are *not* the fixed-point subspace of any subgroup. Examples IV.1 and IV.2 illustrate this.)

Phase space decomposes as a direct sum of irreducible representations of Σ. Isomorphic irreducibles combine to form *isotypic components*. The isotypic component of the trivial representation is $\mathrm{Fix}(\Sigma)$, and each isotopic component is invariant under $DF|_u$. So the eigenvalues of $DF|_u$ can be found by considering its restriction to each isotypic component. More concretely, this decomposition puts $DF|_u$ into block-diagonal form, and we compute the eigenvalues and eigenvectors for each block. This is equivalent to the approach taken in Ref. 36.

A similar approach applies to periodic states near Hopf bifurcation, where stability is governed by Floquet exponents. Here, the calculations require reduction of the system to Poincaré-Birkhoff normal form and exploit spatio-temporal symmetry.[25]

This method is effective for computing transverse eigenvalues of $DF|_u$. For example, it is used in Ref. 14 to analyse a model of binocular rivalry, a type of visual illusion, in which distinct images are shown to each eye. Even in the symmetric case, stability depends not only on network topology, but on the detailed model. One plausible symmetric model for rivalry predicts that perceived states are unstable; a slight modification predicts they are stable.[15]

For chaotic states, transverse stability of an attractor $A \subseteq \Delta$ depends on the averages of transverse eigenvalues with respect to invariant measures on A, especially Sinai-Ruelle-Bowen (SRB) measures.[5,6,44] Intuitively, the dynamic transverse to A may be attracting at some points and repelling at others, and the overall effect depends on this average. The details are complicated because invariant measures are not unique and SRB measures are seldom known to exist.[44]

Typical phenomena include riddled basins,[2] where the basin of attraction of A has a fractal structure; on-off intermittency and blowout bifurcations,[35] where the attractor topology changes discontinuously; chaotic saddles, where the transverse dynamic is repelling;[34] and bubbling,[5,6] where the state repeatedly loses its pattern of synchrony and then regains it.

C. Stability in the absence of symmetry

For general networks without symmetry, the formalism does not provide a comparable degree of control over transverse eigenvalues. It can be shown that every balanced coloring defines a pattern of synchrony that occurs stably for some admissible ODE, but the analogous question for periodic states is less well understood. In particular, it is not known whether there exists a stable periodic solution for every pattern of phase-shift synchrony (see Section III E).

There are three main cases for which stability can be characterized effectively:

(1) Analysis of special models involving specific admissible maps F. See, for example, Refs. 7 and 38.
(2) Exploiting special features of small networks, constraining the form of the admissible maps and their Jacobians.
(3) Feedforward networks, where general results exist because the Jacobian is block-triangular and its eigenvalues are those of the diagonal blocks.

It also seems likely that some general principles apply in cases where admissible maps lift uniquely from a quotient network. However, this idea has not yet been studied in detail.

D. Bifurcations

Bifurcation theory is closely related to stability: indeed, local bifurcation occurs when a state loses stability as a parameter varies. Indeed some areas of application traditionally use "instability" to mean bifurcation. Again, there is a comprehensive theory for symmetric systems, hence also symmetric networks. However, it is important to recognize that symmetric networks do not always behave like generic symmetric ODEs, because the network topology imposes constraints on the variables that occur in the ODE.

In some ways, the situation is more satisfactory than for stability, because there are general phenomena that occur for specific types of stability loss. For example, in Hopf bifurcation, an equilibrium loses stability when a pair of complex conjugate eigenvalues crosses the imaginary axis, creating a bifurcating branch of periodic states. The cause, and the resulting behavior, are well understood, but the conditions for it to happen depend on the eigenvalues of the Jacobian.

Network topology has implications for Hopf bifurcation. For example, in standard Hopf bifurcation, the amplitude along the bifurcating branch typically grows as $\lambda^{1/2}$ for a bifurcation parameter λ. But in a three-cell feedforward chain, the third cell can have an amplitude that grows as $\lambda^{1/6}$.[16,24] Anomalous growth rates also occur for generic steady-state bifurcation at a simple eigenvalue in some multiarrow networks.[41]

VI. RIGID PATTERNS OF SYNCHRONY

We now extend the main results about patterns of synchrony in symmetric networks to general networks, again concentrating on equilibria and periodic states. Some analogous results are known, and others can plausibly be conjectured, for more complex dynamics, such as quasiperiodicity and chaos. We do not discuss these ideas here.

A. Rigidity

Virtually any partition of the cells of a network can be a pattern of synchrony by making a special choice of the admissible vector field. To avoid "accidental" patterns of this kind, we require a form of structural stability. First, recall

Definition VI.1. Consider an ODE

$$\frac{dx}{dt} = F(x) \quad x \in \mathbb{R}^n. \tag{6.1}$$

(a) An equilibrium x_0 of (6.1) is *hyperbolic* if the Jacobian (derivative) of F has no eigenvalue on the imaginary axis.
(b) A periodic state $x(t)$ of (6.1) of period T is *hyperbolic* if it has no Floquet exponent on the imaginary axis.

Hyperbolicity implies that after a small perturbation of the vector field, in case (a) there exists a unique equilibrium $\tilde{x}_0$ near x_0; while in case (b) there exists a unique $\tilde{T}$-periodic orbit $\tilde{x}(t)$ near $x(t)$ in the C^1 topology, with $\tilde{T}$ near T.[31] Thus we can speak of "*the* perturbed equilibrium/periodic cycle."

Now we can define the key concept of rigidity:

Definition VI.2.

Suppose F in (6.1) is admissible for a network.

(a) The pattern of synchrony for an equilibrium or periodic cycle of (6.1) is *rigid* if, for all sufficiently small perturbations, the perturbed equilibrium or periodic cycle has the same pattern of synchrony.
(b) A pattern of phase shifts for a periodic cycle of (6.1) is *rigid* if, for all sufficiently small perturbations, the perturbed periodic cycle has the same pattern of phase shifts (as fractions of the period).

Rigidity is not typical of phase shifts in general dynamical systems. However, in a symmetric ODE, the pattern of synchrony for an equilibrium or periodic cycle determined by the orbits of its isotropy subgroup is also rigid. The pattern of phase shifts for a periodic cycle determined by the H/K Theorem is rigid.[18–20]

In the equilibrium case, we can classify rigid patterns of synchrony[27]

Theorem VI.3.

Let x_0 be a hyperbolic equilibrium of an admissible ODE (6.1). Then the pattern of synchrony for x_0 is rigid if and only if it corresponds to a balanced coloring.

In the periodic case, we can classify rigid patterns of synchrony and rigid patterns of phase shifts, subject to a mild technical condition. This result combines the results of Refs. 18 and 19 with a theorem of Ref. 43. It is an analog for general networks of the H/K theorem, in which K becomes a

balanced coloring and H/K acts on the corresponding quotient network.

Theorem VI.4.

Let $x(t)$ be a hyperbolic periodic cycle of an admissible ODE (6.1). Suppose that the network is path-connected, and all cell equivalent cells are input equivalent. Then:

(1) *If the pattern of synchrony for $x(t)$ is rigid, it corresponds to a balanced coloring.*
(2) *If the pattern of phase shifts for $x(t)$ is rigid, then the quotient network corresponding to the pattern of synchrony has a cyclic symmetry group, and the pattern of phase shifts is that of a rotating wave induced by this symmetry group.*
(3) *Conversely, any pair consisting of a balanced coloring and a cyclic group of symmetries of the quotient network determines a pattern of synchrony and a pattern of phase shifts.*

Part (2) is remarkable because it deduces a global conclusion, cyclic symmetry, from local comparisons of phase shifts. It is a consequence of the rigid phase shift theorem,[18,19] which states that, subject to technical conditions, phase-shifted cells have inputs related by the same phase shift.

Example VI.5.

Consider the network of Figure 3 (left). This has a rigid pattern of phase shifts of the form

$$(x(t), x(t+T/3), x(t+2T/3), x(t+T/3), x(t+2T/3)). \tag{6.2}$$

On the quotient, the pattern of synchrony for this state is $\{1\}, \{2, 4\}, \{3, 5\}$ which is balanced. The quotient network is shown in Figure 3 (right), and this has $\mathbb{Z}_3$ symmetry. The pattern of phase shifts is that of a rotating wave with $(H, K) = (\mathbb{Z}_3, 1)$. This explains the periodic state described in Example I.3.

Example VI.6.

Different patterns of phase shifts on the same network may arise from different balanced colorings and different quotient networks. Figure 10 is an example. Pattern (6.1) comes from the $\mathbb{Z}_3$ symmetry of the 4-cell network, with a trivial pattern of synchrony whose quotient network is the same as the original. Pattern (6.2) comes from the $\mathbb{Z}_2$ symmetry of the 2-cell quotient network, corresponding to a nontrivial pattern of synchrony for the 4-cell network.

It is not possible to explain both patterns using the same symmetry group, because that would have to contain $\mathbb{Z}_6$, which is not the symmetry group of any network with four or fewer cells.

[1]J. W. Aldis, "A polynomial time algorithm to determine maximal balanced equivalence relations," Int. J. Bifurcation Chaos Appl. Sci. Eng. **18**, 407–427 (2008).
[2]J. C. Alexander, I. Kan, J. A. Yorke, and Z. You, "Riddled basins," Int. J. Bifurcation Chaos Appl. Sci. Eng. **2**, 795–813 (1992).
[3]F. Antoneli and I. Stewart, "Symmetry and synchrony in coupled cell networks 1: Fixed-point spaces," Int. J. Bifurcation Chaos Appl. Sci. Eng. **16**, 559–577 (2006).
[4]F. Antoneli and I. Stewart, "Symmetry and synchrony in coupled cell networks 2: Group networks," Int. J. Bifurcation Chaos Appl. Sci. Eng. **17**, 935–951 (2007).
[5]P. Ashwin, J. Buescu, and I. Stewart, "Bubbling of attractors and synchronisation of chaotic oscillators," Phys. Lett. A **193**, 126–139 (1994).
[6]P. Ashwin, J. Buescu, and I. Stewart, "From attractor to chaotic saddles: A tale of transverse instability," Nonlinearity **9**, 703–737 (1996).
[7]V. Belykh, I. Belykh, and M. Hasler, "Hierarchy and stability of partially synchronous oscillations of diffusively coupled dynamical systems," Phys. Rev. E **62**, 6332 (2000).
[8]I. Belykh, V. Belykh, K. Nevidin, and M. Hasler, "Persistent clusters in lattices of coupled nonidentical chaotic systems," Chaos **13**, 165 (2003).
[9]I. Belykh and M. Hasler, "Mesoscale and clusters of synchrony in networks of bursting neurons," Chaos **21**, 016106 (2011).
[10]P-L. Buono, "Models of central pattern generators for quadruped locomotion II: Secondary gaits," J. Math. Biol. **42**, 327–346 (2001).
[11]P. L. Buono and M. Golubitsky, "Models of central pattern generators for quadruped locomotion: I. Primary gaits," J. Math. Biol. **42**, 291–326 (2001).
[12]J. J. Collins and I. Stewart, "Coupled nonlinear oscillators and the symmetries of animal gaits," J. Nonlin. Sci. **3**, 349–392 (1993).
[13]C. Diekman and M. Golubitsky, "Network symmetry and binocular rivalry experiments," J. Math. Neuro. **4**(12) (2014).
[14]C. Diekman, M. Golubitsky, T. McMillen, and Y. Wang, "Reduction and dynamics of a generalized rivalry network with two learned patterns," SIAM J. Appl. Dyn. Syst. **11**, 1270–1309 (2012).
[15]C. Diekman, M. Golubitsky, and Y. Wang, "Derived patterns in binocular rivalry networks," J. Math. Neuro. **3**(6) (2013).
[16]T. Elmhirst and M. Golubitsky, "Nilpotent Hopf bifurcations in coupled cell systems," SIAM J. Appl. Dyn. Syst. **5**, 205–251 (2006).
[17]M. Golubitsky, L. Matamba Messi, and L. E. Spardy, "Symmetry types and phase-shift synchrony in networks," Physica D **320**, 9–18 (2016).
[18]M. Golubitsky, D. Romano, and Y. Wang, "Network periodic solutions: Full oscillation and rigid synchrony," Nonlinearity **23**, 3227–3243 (2010).
[19]M. Golubitsky, D. Romano, and Y. Wang, "Network periodic solutions: Patterns of phase-shift synchrony," Nonlinearity **25**, 1045–1074 (2012).
[20]M. Golubitsky and I. Stewart, *The Symmetry Perspective* (Birkhäuser, Basel 2000).
[21]M. Golubitsky and I. Stewart, "Homeostasis, singularities and networks," J. Math. Biology (published online).
[22]M. Golubitsky, I. Stewart, P.-L. Buono, and J. J. Collins, "A modular network for legged locomotion," Physica D **115**, 56–72 (1998).
[23]M. Golubitsky, I. Stewart, P.-L. Buono, and J. J. Collins, "Symmetry in locomotor central pattern generators and animal gaits," Nature **401**, 693–695 (1999).
[24]M. Golubitsky, I. Stewart, and M. Nicol, "Some curious phenomena in coupled cell networks," J. Nonlinear Sci. **14**, 207–236 (2004).
[25]M. Golubitsky, I. Stewart, and D. G. Schaeffer, *Singularities and Groups in Bifurcation Theory: Vol. II*, Applied Mathematical Sciences 69 (Springer, New York, 1988).
[26]M. Golubitsky, I. Stewart, and L. J. Shiau, "Spatio-temporal symmetries in the disynaptic canal-neck projection," SIAM J. Appl. Math. **67**, 1396–1417 (2007).
[27]M. Golubitsky, I. Stewart, and A. Török, "Patterns of synchrony in coupled cell networks with multiple arrows," SIAM J. Appl. Dyn. Syst. **4**, 1396, 78–100 (2005).
[28]F. Hoppensteadt, *An Introduction to the Mathematics of Neurons* (Cambridge University Press, Cambridge, 1986).
[29]K. Josić and A. Török, "Network architecture and spatio-temporally symmetric dynamics," Physica D **224**, 52–68 (2006).
[30]H. Kamei and P. J. A. Cock, "Computation of balanced equivalence relations and their lattice for a coupled cell network," SIAM J. Appl. Dyn. Syst. **12**, 352–382 (2013).
[31]A. Katok and B. Hasselblatt, *Introduction to the Modern Theory of Dynamical Systems* (Cambridge University Press, Cambridge, 1995).
[32]Y. Kuramoto, *Chemical Oscillations, Waves, and Turbulence* (Springer, Berlin, 1984).
[33]G. McCollum and R. Boyle, "Rotations in a vertebrate setting: Evaluation of the symmetry group of the disynaptic canal-neck projection," Biol. Cybern. **90**, 203–217 (2004).
[34]H. Nusse and J. A. Yorke, "Analysis of a procedure for finding numerical trajectories close to chaotic saddle hyperbolic sets," Ergodic Theory Dyn. Syst. **11**, 189–208 (1991).

[35]E. Ott and J. C. Sommerer, "Blowout bifurcations: The occurrence of riddled basins and on-off intermittency," Phys. Lett. A **188**, 39–47 (1994).
[36]L. M. Pecora, F. Sorrentino, A. M. Hagerstrom, T. E. Murphy, and R. Roy, "Symmetries, cluster synchronization, and isolated desynchronization in complex networks," Nat. Commun. **5**, 4079 (2013).
[37]C. A. Pinto and M. Golubitsky, "Central pattern generators for bipedal locomotion," J. Math. Biol. **53**, 474–489 (2006).
[38]A. Y. Pogromsky, "A partial synchronization theorem," Chaos **18**, 037107 (2008).
[39]A. Y. Pogromsky, G. Santoboni, and H. Nijmeijer, "Partial synchronization: From symmetry towards stability," Physica D **172**, 65–87 (2002).
[40]I. Stewart, "The lattice of balanced equivalence relations of a coupled cell network," Math. Proc. Cambridge Philos. Soc. **143**, 165–183 (2007).
[41]I. Stewart and M. Golubitsky, "Synchrony-breaking bifurcation at a simple real eigenvalue for regular networks 1: one-dimensional cells," SIAM J. Appl. Dyn. Syst. **10**, 1404–1442 (2011).
[42]I. Stewart, M. Golubitsky, and M. Pivato, "Symmetry groupoids and patterns of synchrony in coupled cell networks," SIAM J. Appl. Dyn. Syst. **2**, 609–646 (2003).
[43]I. Stewart and M. Parker, "Periodic dynamics of coupled cell networks II: cyclic symmetry," Dyn. Syst. **23**, 17–41 (2008).
[44]L.-S. Young, "What are SRB measures, and which dynamical systems have them?," J. Stat. Phys. **108**, 733 (2002).